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Source: *The Auk*, Vol. 112, No. 4 (Oct., 1995), pp. 1064-1066

Published by: [American Ornithologists' Union](#)

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Received 6 January 1995, accepted 10 May 1995.

The Auk 112(4):1064-1066, 1995

Accelerational Implications of Hummingbird Display Dives

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Gravitationally induced forces and hydrostatic pressures in blood columns are well known to impose hypertension in various animals (e.g. giraffes [*Giraffa camelopardalis*], Hargens 1987; climbing snakes, Lillywhite 1987). Less well studied is transient imposition of high forces and dynamic induction of physiological pressures above resting values. In birds, rapid turns, sudden decelerations, and high-speed appendicular motions can impose substantial external and internal forces (e.g. Larimer and Dudley 1994) and, concomitantly, elevated internal pressures. Hummingbirds are particularly known for engaging in rapid display behaviors, which can be used in courtship toward a potential mate or in intra- and interspecific aggression. Such displays often incorporate a species-specific diving component at variable speeds and curvature radii at the bottom of the dive (Bent 1940, Wagner 1946, Johnsgard 1983, Miller and Inouye 1983, Stokes and Stokes 1989, Tamm et al. 1989, Scott 1993). Common Nighthawks (*Chordeiles minor*) also have high-speed display dives with low-frequency acoustic components (Miller 1925, Bent 1940, Breland 1972).

The display behaviors of Allen's Hummingbirds (*Selasphorus sasin*; Pearson 1960) and Anna's Hummingbirds (*Calypte anna*; Stiles 1982) are particularly spectacular and are among the best described of avian display dives. In both species, the display usually begins with a long steep dive initiated 20 to 35 m above a conspecific bird. When the diving bird is about 1 m of the display target and moving probably at maximal velocity, an abrupt pullout ensues during which radial accelerations must be substantial. Seg-

ments of the display are accompanied by species-specific vocalizations.

Because of the high velocities associated with hummingbird displays, it is of interest to calculate centrifugal forces and the corresponding accelerations associated with the pullout phase of the dives. Although dive trajectories have not been described quantitatively, the pullout consists of motion along an approximately circular arc leading into the ascent portion of the display (Stiles 1982). Thus, one can estimate radial forces and accelerations assuming circular motion. For this case, centrifugal force is given by mv^2/r , where m is the object mass, v is the velocity, and r is the local radius of curvature. Centripetal acceleration is correspondingly given by v^2/r . In circular motion, the centrifugal force is directed outwards and is orthogonal to the local tangent, whereas body orientations during diving are likely to be parallel to the flight trajectory (e.g. see Stiles 1982).

Available information on display dive velocities and geometry in *S. sasin* and *C. anna* is summarized in Table 1. Radii of curvature for dives of *C. anna* were approximated from graphic representations (see Stiles 1982); dive velocities reported by Stiles (1982) include a mean and maximum values. For *S. sasin*, the reported mean velocity at the bottom of the dive was used in acceleration and force calculations; although dive geometry was not specified in the original paper, a possible range of values for the radius of curvature can be estimated from description of the dive in relation to local landmarks (see Pearson 1960).

Calculated centripetal accelerations at the bottom of hummingbird display dives equal 70 to 100 m/s²

TABLE 1. Species identification, body weight, dive velocity, radius of curvature, calculated centrifugal forces, and radial accelerations during display dives of two hummingbird species. Body-weight data represent average values for males (see Johnsgard 1983). Dive velocity indicates mean (maximum) velocity for entire dive (*C. anna*), or mean value for bottom portion of the dive (*S. sasin*). Likely range for radius of curvature given for *S. sasin*.

	<i>Calypte anna</i>	<i>Selasphorus sasin</i>
Body weight (N*)	0.042	0.035
Velocity (m/s)	17.0 (maximum 20)	17.6
Radius (m)	4	3-4
Acceleration (m/s ²)	72 (maximum 100)	77-103
Force (N)	0.31 (maximum 0.43)	0.27 (maximum 0.36)
Reference	Stiles (1982)	Pearson (1960)

* N, Newton.

(Table 1), which correspond to approximately 7 to 10 G. Such accelerations potentially can induce deleterious physiological responses. In humans, for example, accelerations of 3 to 4 G applied longitudinally to the body axis can curtail cerebral blood perfusion, as well as limit venous return from the extremities; vision and respiration also are affected (Blomqvist and Stone 1983, Guyton 1991, McCloskey et al. 1992). However, the radial accelerations in display dives of hummingbirds are approximately transverse to the longitudinal body axis, a configuration in which, at least in humans, much higher accelerations can be tolerated without adverse effect (Guyton 1991). Also, the small size of hummingbirds suggests that hydrostatic pressures induced along fluid columns will be much smaller for comparable accelerations. In the ascending portion of the hummingbird display dive, however, transient decelerations associated with changes in the initially high translational velocity could be substantial and will be directed along the longitudinal body axis. No kinematic data are available to estimate the magnitude of such effects, and the high flight velocities ensure that such decelerations will be imposed over periods of very short duration.

Concomitant with high centripetal accelerations, centrifugal forces associated with pullouts of hummingbirds display dives are substantial and correspond to transient values approximately 10 times the body weight (Table 1). Such forces acting on the wings and body may predispose diving behavior to sound production through aerodynamic vibration of tail feathers (Allen's Hummingbird; Aldrich 1956) and wing feathers (Common Nighthawk; Miller 1925). Wing damage at the shoulder joint also is a possibility; centrifugal forces on the body could combine with high lift forces produced by the wings to impose unacceptably high torque at the wing base. No reports exist, however, of such injuries; behavioral and/or morphological adaptations therefore, may, be sufficient to avoid such damage.

Considerations of adverse accelerational consequences of hummingbird display dives suggest a more

general observation. Whereas the metabolic costs of sexually selected displays are often high, additional biomechanical features of high-speed motion also may impose selective constraints on display evolution. In hummingbirds, rapid turns and dives as part of advertisement displays undoubtedly incur high energetic expenditure, but potentially can induce deleterious physiological and biomechanical effects as well.

Acknowledgments.—We thank R. H. Barth, C. Pease, and P. E. Scott for useful discussions, and J. Major for assistance with the literature.

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Received 22 November 1994, accepted 8 March 1995.

The Auk 112(4):1066–1070, 1995

Xiphorhynchus striatigularis (Dendrocolaptidae): *Nomen monstrositatum*

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On 18 November 1894, Frank B. Armstrong collected an unusual woodcreeper near Altamira, Tamaulipas, Mexico. This specimen was sent with others for identification to the United States National Museum during the winter of 1894–1895 (Richmond 1896), and was eventually described as a new species, *Dendroornis* [= *Xiphorhynchus*] *striatigularis*, based on its distinct plumage (Richmond 1899; USNM 135157; 18 November 1894, Alta Mira, Tamaulipas; female).

Despite the fact that this region can now be considered rather well collected, this taxon continues to be represented only by the unique type, suggesting that it is: (A) a very rare and now probably extinct (but valid) species; (B) the hybrid product of two valid species; or (C) an aberrant individual of a valid species (cf. Graves 1990). *Xiphorhynchus striatigularis* has received little attention since its description. Some authors simply list the taxon with little or no discussion (e.g. Ridgway 1911, Cory and Hellmayr 1925, Peters 1951, Blake 1953, Miller et al. 1957), while others either exclude it altogether (Edwards 1972, 1989, Peterson and Chalif 1973), or consider it an aberrant *X. flavigaster* (AOU 1983, Sibley and Monroe 1990). No evidence has been presented to favor any of the above hypotheses or treatments. My examination attempts to resolve the nature of the unique type.

Methods.—It is assumed that woodcreeper species occupying the region around Altamira (lower elevations of northeastern Mexico) will be morphologically distinct and that, if valid, *X. striatigularis* would exhibit a size and shape different from that of same-sex individuals of other species in this area. This assumption would not be robust for all taxonomic groups or geographic areas. It seems robust here, however, because the center of species diversity in *Xiphorhyn-*

chus occurs in South America (Sibley and Monroe 1990), and no cryptic species of Dendrocolaptidae are known in northern Middle America. Armstrong's handwriting is apparent on the original label of *X. striatigularis*, suggesting that the data there are correct (see Oberholser 1974:8).

The hypothesis of hybrid origin does not make morphological predictions. Although it would seem likely, intermediacy in body form might not occur, even if the individual is an F₁ hybrid (G. Graves pers. comm.). If *X. striatigularis* is an aberrant individual of a valid species and the aberrancy is restricted to pigment deposition in the plumage (the latter is the basis for this taxon; Richmond 1899), its external morphometrics should match one of the species occurring in the region.

Diagnosis of this unique type is aided by the fact that southern Tamaulipas is near the northerly limits of the Dendrocolaptidae, and only two species (of two genera) currently occur in the region where the unique type was taken: *X. flavigaster* and *Lepidocolaptes affinis*. A third species, *L. souleyetii*, reaches central Veracruz, and is included in this study. Three other dendrocolaptids occur in northern Mexico, but were not included in this analysis. *Xiphocolaptes promeropirhynchus* and *Sittasomus griseicapillus* were excluded because their sizes, ranges, and plumage characteristics preclude their involvement in the latter two hypotheses presented above. I excluded *Xiphorhynchus erythropygius* because of its range, its montane elevational preference in Mexico, and a lack of evidence in the plumage of *X. striatigularis* of a contribution from *erythropygius*.

The unique type of *X. striatigularis* is in basic plumage, and its distinct plumage characteristics are not